

SHORT NOTES

Survival of crinoid stalk fragments and its taphonomic implications

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Abstract. Paleontological evidence indicates that crinoids (sea lilies: Echinodermata) were a major constituent of Paleozoic and Mesozoic shallow-marine communities (Meyer and Macurda, 1977 ; Cain, 1968). In the fossil record crinoid stalks usually occur in much greater abundance than other body parts such as arms and calyces. This difference has been attributed to selective preservation, the result of post-mortem process of fossilization or taphonomy (Baumiller and Ausich, 1992 ; Moore and Jeffords, 1968). Our observation of living crinoids in aquaria demonstrates that stalk fragments detached and isolated from a living crinoid survive more than one year, whereas other body parts tend to disarticulate rapidly. Such long survival of stalk fragments of crinoids firstly explains the dominance of crinoid stalks over other body parts in the fossil record, and secondly, and more importantly, it strongly suggests that such detached fossil stalks, as well as stalk pieces observed on today's sea floor, continued living for a long time, and were not dead body parts as previously considered.

Key words : Crinoid, taphonomy

Introduction

It is well known that among crinoid skeletal parts stalk (or stem) fragments predominate in shallow-marine deposits, whereas other skeletal parts, such as arms and calyces are rarely found (Moore and Jeffords, 1968). Given the original proportions of skeletal elements in crinoids, it is a mystery that stalk fragments are so predominant whereas other parts of disarticulated crinoid skeletons are rare.

Recent observations by submersibles and underwater cameras have demonstrated that detached stalk fragments of modern stalked crinoids are often found in association with entire crinoids (Conan *et al.*, 1981 ; Fujita *et al.*, 1987 ; Messing *et al.*, 1988). Such stalks without crowns sometimes stand erect off the substrate, grasping gravels and other hard objects by the appendages called cirri, as if they still held their crowns. During growth, new stalk plates are formed at the top of the stalk just below the crown (Breimer, 1978), and the distal (old) part of the stalk is repeatedly detached from the main stalk and left on the sea floor (Rasmussen, 1977). Fossil stalks are abundant in Paleozoic and Mesozoic shallow-water deposits. Such fossil stalk fragments were thought to be selectively preserved after death whereas the other body parts were disarticulated and lost (Baumiller and Ausich, 1992 ; Moore and Jeffords, 1968). However, other than experiments on the post-mortem disintegration of the isocrinid stalks (Baumiller and Ausich, 1992), there has been no information about the "fate" of such

isolated stalk fragments. The purpose of the present study is to test if these autotomized and isolated stalk fragments remain alive for a long time, and also to consider the implications of the results for the taphonomy of crinoid skeletons.

Material and methods

We have collected adult specimens of the modern stalked crinoid *Metacrinus rotundus* Carpenter from the depths of 135-150 m in NE Suruga Bay, central Japan. Specimens were transferred to a large, temperature-controlled aquarium (13°C) at the Misaki Marine Biological Station, University of Tokyo, within several hours after capture. They were kept alive for over one year (Amemiya and Oji, 1992). During this period, most specimens autotomized their distal stalks as well as their crowns, and the isolated stalk fragments were left on the bottom of the aquarium.

For comparison with the autotomized and isolated fragments of stalk, the distal stalks with two to three nodals were dissected at an articulation below a nodal by a razor blade, and they were also kept on the bottom of the aquarium. We have also examined the nucleus and ligament using histochemical and fluorescent dye staining to see if a stalk left for ten months and another stalk dissected and left for 13 months in the aquarium were living. Stalk fragments were fixed and decalcified with Bouin solution, and subsequently embedded in paraffin and stained with a fluorescent dye, Hechst 33258, or with hematoxylin-eosin after sectioning.

As a control, another distal stalk fragment, which was dissected directly from an intact specimen with arms and a calyx, was immediately fixed and processed as above for comparison.

Results

The autotomized fragments usually range from 8 to 17 cm long, with four to eight nodal plates. They were apparently detached at almost flat articulations below a nodal plate, which is believed to be a specialized articulation for stalk autotomy (Emson and Wilkie, 1980). One specimen of *Metacrinus rotundus* collected on Oct. 7, 1989 detached its distal stalk within several days of capture. The detached stalks have held the same postures and some remained attached to pebbles by the cirri for approximately one year (Figure 1).

The stalks dissected by a razor blade below a nodal plate, also remained fully articulated for 10 to 13 months, indicating that ligamentary fibers connecting each plate of the stalks and cirri had not disintegrated or degraded during this period.

By the histochemical and fluorescent dye staining, the nuclei in the autotomized stalk fragments were all well preserved and stained clearly with both stains (Figure 2a, c)

and they were similar to the control (Figure 2d), indicating that the cells were living. The collagen-like fibers composing the stalk ligament in the autotomized stalk fragments left in the aquaria (Figure 2b) were also well preserved, supporting the idea that the fragments were still viable. Dissected stalk fragments which were left in the aquarium for about a year showed similar characteristics in the stained thin sections.

Discussion

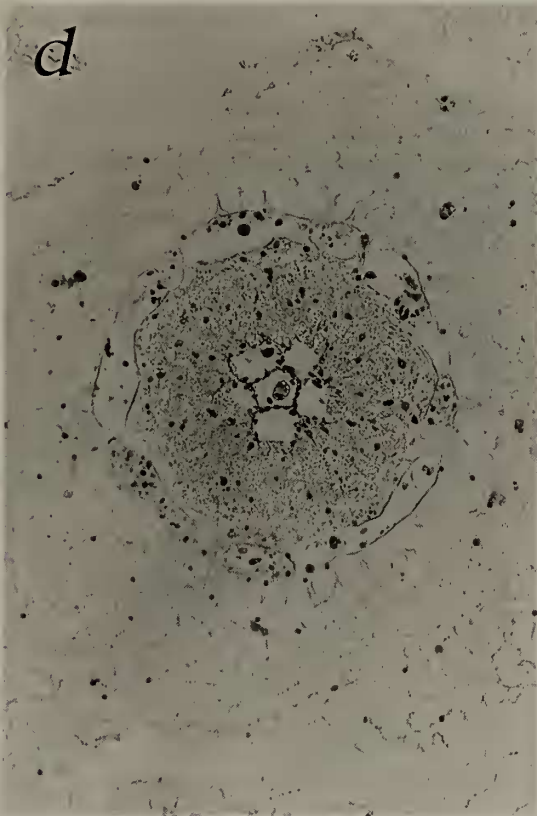
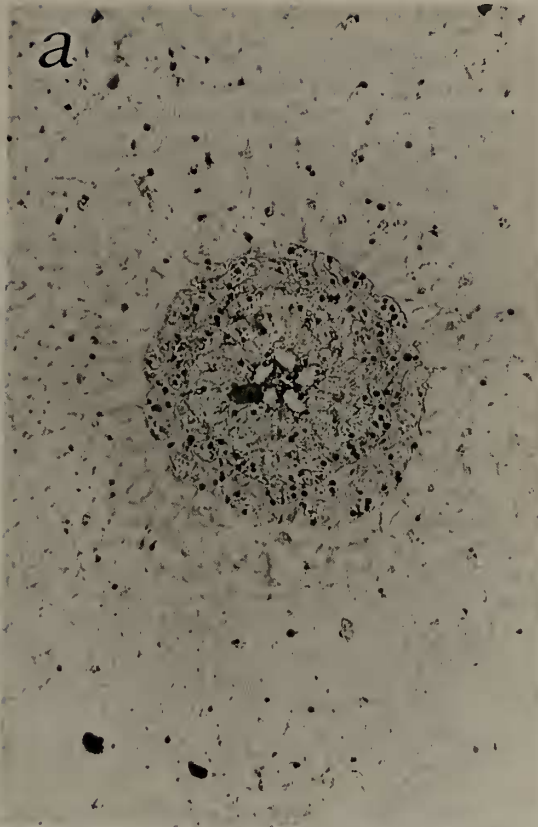
Our findings strongly suggest that fragmented stalks can live for more than one year in the natural environment. Also it suggests that similar isolated isocrinid stalks observed in the crinoid habitat by submersibles (Conan *et al.*, 1981; Messing *et al.*, 1988) and underwater photographs (Fujita *et al.*, 1987) were also living.

In contrast to the strong regeneration power in the arms and visceral mass (Emson and Wilkie, 1980; Meyer, 1985; Amemiya and Oji, 1992) of crinoids, there has been no record of apparent stalk regeneration in Recent stalked crinoids. At least as regards isocrinid crinoids, the isolated stalk fragments were presumably living passively, without regenerating or growing. However, an Ordovician stalk with an



Figure 1. One of the specimens collected on Oct. 7, 1989 autotomized its distal stalk as well as its crown several days after capture (Left). The autotomized stalk fragments (right and center) were derived not only from the specimen on the left side, but also from other specimens. They retained almost the same posture and some remained attached to pebbles by cirri for approximately one year. Arrows indicate such autotomized stalks. Photo taken on Oct. 23, 1990. The width of the picture is approximately 60 cm.

Figure 2. Micrographs of the stalk of *Metacrinus rotundus*. Magnification $\times 108$ in a, b and d; $\times 44$ in c. **a**: Cross section of axial area of stalk which autotomized from the main body and was left in the aquarium for approximately one year. Note well-stained nuclei in and around the axial canal. **b**: Longitudinal section of the different stalk fragment with two stalk plates, which was also autotomized and left in the aquarium for approximately one year. Through-going ligaments still attach two stalk plates (above and below) tightly. **c**: Epithelium and outer area of the cross section of the stalk. The same stalk fragment as in b. **d**: Cross section of axial area of stalk which was not autotomized and directly cut from an intact specimen. No significant difference is observed between this section and the autotomized one (a).



anomalous form was recently reinterpreted as a regenerated stalk (Ausich and Baumiller, 1993).

Fossil stalks are often abundant in Paleozoic and Mesozoic strata. Many of these occurrences represent crinoid banks formed in a shallow-water environment (Meyer and Macurda, 1977). Most of the stalk fragments consist of a series of articulated stalk plates, indicating that ligamentary fibers united these plates before their burial in the sediment. The present results, as well as the Ordovician anomalous fossil stalk, suggest that at least some of these stalk fragments have/had the ability to remain alive for a long time on the sea floor, despite lacking any food-gathering organ. The presence of stalks and the absence of calyces and arms in fossil deposits do not suggest that these stalks were dead prior to fossilization. Instead, the successful preservation of crinoid stalks may reflect their longer survival and later time of death than their crowns. Arms tend to be disarticulated rapidly into small skeletal grains, and thus have a smaller chance to be preserved intact, whereas stalk fragments with at least several columnal plates remain integrated for a long time, possibly resulting in contrasting chance of preservation between arm and stalk elements in the fossil record.

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